2. PENTOXYLON PLANT: A RECONSTRUCTION AND INTERPRETATION

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Abstract

Considering the constant association of vegetative and fertile organs: *Pentoxylon* (stem), *Nipaniophyllum* (leaf), *Sahnia* (pollen organ) and *Carnoconites* (seed cone), it has been tempting to envisage as to how the whole *Pentoxylon* plant might have looked like by piecing together. Also it is speculated in what kind of possible habitation or surrounding it could have been thrived. However, it seems very likely that this branched shrubby plant could have attained the height of possibly a small tree possessing supposedly a robust crinkled stem devoid of leaf bases probably thrown off with the maturity. Further, the branches presumably have been portrayed arising and dichotomizing at the extremity of stem whereas the branch scars due to shedding are shown at lower level. The dichotomized branches bear long and short shoots. The long shoots demonstrate sparsely placed leaf cushions while the short shoots have closely placed leaf cushions. The foliage and fertile organs are borne on different kinds of short shoots. However, the attachment on short shoots is indicative of these diverse plant organs belonging to the same plant. The woody short shoots having spirally arranged persistent rhomboid leaf base-cushions depict terminally dichotomizing branchlets each bearing broadly conical head. The female cone *Carnoconites* containing spirally arranged seeds possessed their micropyles pointing outwards. The outer fleshy and inner stony layer are well developed and nucellus is free from the integument. The short shoots of thick parenchymatous cells terminate into pollen cone *Sahnia* borne on a collar like structure formed by the raised margin of receptacle. The pollen organ consists of persistent microsporangiophores bearing short branch with several stalked rounded sporangia containing oval monocolpate pollen grains showing longitudinal dehiscence. The slender short shoots which are borne in the axils of long shoots generally bear in apical portion bunch of simple rather stiff, coriaceous, strap-shaped leaves of *Nipaniophyllum*. The plants were deciduous dropping off the leaves in their entirety. Whether the *Pentoxylon* plant was monoecious or dioecious, for the present, it has been taken as to be monoecious because *Sahnia* though very rare has always been found intimately associated with *Carnoconites* which generally occurs detached enormously among other plant remains. Further, the occurrence of *Pentoxylon* plant has been noted in overwhelming majority in the floral assemblage of *Nipania*, Rajmahal Hills, India, wherein the representation of *phycophytes, mycophytes, pteridophytes*, and *cycadophytes* are less frequent. However, the conifers are quite common. The advent of *pentoxylopsids* mark a floral change, thereby confirming the younger age for *Nipania* deposits among the various fossil sites of Rajmahal Hills. Taking the floral composition of *Nipania* as a whole, it appears, that the vegetation flourished along the lake margins on volcanic terrain under subtropical humid climate. Besides, the discovery of *Pentoxylon* plant from Australia, New Zealand and Antarctica is quite significant, keeping in view the free dissemination of plant all over the Gondwana countries until the breakup of this supercontinent.

Key words: Pentoxylon, macrofossil, reconstruction, Gondwana.

Introduction

Our inquisitiveness as to how the *Pentoxylon* plant must have looked like inspired us to propose the reconstruction presented here. The consistent co-occurrence of isolated parts of pentoxylopsids and their structure similarity suggested that they belong to one

and the same plant. Since the association of the plant parts were in sufficient frequency, it has been ventured to piece them together in the form of an entire plant.

The pentoxylopsids come from the locality of Nipania in Rajmahal Hills, Bihar which was first discovered in situ by HOBSON (1928 in PASCOE, 1929). From this collection SAHNI (in PASCOE, 1929) reported for the first time the plant fossil-leaves preserved in cherts in the form of silicified blocks. Further, SAHNI (1932) traced the affinity of these leaves. However, in subsequent years from these white or cream-coloured rocks (weathering rusty brown) at the head of ravine about half a mile east of *Nipania* Village. SAHNI and RAO (1933) made the first collection and enlisted a good many plant fossils. Since then in series of publications (SAHNI 1932, 1935, 1938, 1948; SAHNI and RAO, 1933; RAO 1935, 1936, 1943a,b,c, 1947, 1974; SRIVASTAVA 1935, 1937, 1944, 1946; VISHNU-MITTRE 1952, 1953, 1955, 1958, 1969; SINGH 1957) contributed to the paleofloristics of *Nipania.*

The diverse plant organs represent portions of two species because the seed cone - *Carnoconites* known by two species *C. compactus* and *C. rajmahalensis* WIELAND described by SRIVASTAVA (1944) and BOSE et al. (1985). So as the leaf-genus differentiated on the basis of size is also represented by *Nipaniophyllum raoi* and *N. hobsonii.* However, the stem genus *Pentoxylon* has been known so far only by one species: *P. sahnii.* SHARMA (1969, 1973a,b, 1974, 1975, 1979, 1980, 1996) made a critical observation of branching pattern and anatomy of *Pentoxylon sahnii* inclusive of dwarf shoots. The polymorphic branch system of *Pentoxylon*-plant compose of long shoots (without leaf bases), thin shoots (with sparse leaf bases) and dwarf shoots bearing fertile organs (with closely placed leaf bases). The pollen organ *Sahnia* was first described and discovered by VISHNU-MITTRE (1953) and later BOSE et al. (1985) made comprehensive observations based on several specimens. SUTHER and SHARMA (1988) interpreted differently while reconstructing this pollen organ.

From these various parts it is tempting to envisage a *gymnospermous* plant perhaps not too tall with foliage borne on the stem. In this reference, the first reconstruction was proposed by SAHNI (1948) which substantiated that *Nipaniophyllum raoi* was borne on the female shoot possessing *Carnoconites* besides he also dealt with the systematic position and could visualize that the *Pentoxylon* plant should have been a branched shrub or xerophytic small tree in habit. The inference for xeric nature could be deduced on the basis of deciduous nature of leathery leaves and succulent sarcotesta of the *Carnoconites.* The unisexual flower were borne at the end of lateral dwarf shoots. The young flowers among the terminal branch of simple strap-shaped leaves were protected by scale leaves which were shed by the formation of an abscission layer quite identical to the one formed by foliage. Leaf bases probably were thrown off from the older stem with the formations of bark maturation.

Another reconstruction attempt came into light when ROZEFELDS (1982) contemplated it to be like a medullosan tree an extremely speculative interpretation based upon the specimens discovered from Early Cretaceous of Australia. Later Mary WHITE (1990) reconstructed the *Pentoxylon australica* somewhat similar to a *cycadophytic* plant. Lately SHARMA (1996, text-fig. 1J) presented a reconstruction of *Pentoxylon sahnii*-plant as a small tree with multimorphic branches, polystelic vasculature and diploxylic bundle of *Nipaniophyllum* leaves. However, it was based upon vegetative parts, no fructification could be depicted, henceforth, it would not be categorised along with the whole plant reconstruction.

Evidence of reconstruction

With foregoing records of reconstruction of *Pentoxylon*-plant, the evidence of our attempt for the present reconstruction has been based on the constant association of long and dwarf shoots, male and female cones from the type locality of *Nipania* as well as different localities of Rajmahal Hills. Morphological and anatomical similarities that is pentamerous arrangement of vascular bundles in long shoot, leaf bearing shoot and dwarf shoot possessing female cones have proven that the vegetative and fertile organs come from one and the same plant. Additionally, the long shoots of *Pentoxylon*-plant in its helical arrangement of leaf scars bearing 5-9 vascular traces are identical to the leaf scars of foliage male and female shoots. SRIVASTAVA (1946, pl. 3, figs. 23-25) has shown the foliage dwarf shoot coming off from longshoot of *Pentoxylon* and anatomically also observed the presence of the ground tissue quite common in both type of shoots. Further, isolated pedicel of peduncle depict the same three bundles the two laterals of larger size than the third middle one and those are similar to the five groups of cortical bundles of peduncle supplied to the pedicel of five cones.

Habit

As the *Pentoxylon*-plant bears long and short (dwarf) shoots which is usually frequent among *Ginkgo*-tree that is why we could envisage that the plant should have been of arborescent habit. It could be further substantiated by evidences like mechanical cells in the outer cortex, nests of sclerotic cells and stone cells in the inner cortex. Apart from the occurrence of periderm, coniferous type secondary xylem and dwarf shoots bearing cone are some of the indirect indication of its tree nature. In the reconstruction presented here, the stem of *Pentoxylon*-plant is hypothetically drawn and its height has been assessed to be of 2-6 metres supposedly robust and crinkled. The branches presumably have been portrayed arising and dichotomizing at the extremity of stem in the form of long shoots which ultimately ramifies into dwarf (short) shoots bearing terminally or laterally borne foliage or male and female cones. The long shoots (*Pentoxylon sahnii* SRIVASTAVA 1946) bearing short shoots in the axil of sparsely placed leaf-cushions on maturity depict dwindling of leaf scars and shoot scars due to periderm formation. In the transverse section of long shoots, generally five bundles are present associated with epidermis, compact outer cortex, parenchymatous inner cortex with nests of sclerotic and stone cells. Presence of cortical bundles has been marked with little variations: one with centrifugal secondary xylem associated with a few centripetal tracheids where as the other only with the centripetal secondary xylem. However, main bundles usually consists of less centrifugal but strong centripetal secondary xylem. Unusually centripetal and centrifugal xylem are of equal development in first season growth. Afterwards the growth is more towards centripetal side than centrifugal side. Secondary phloem is preserved outside the xylem of main bundles.

Nipaniophyllum a simple, strap-shaped leaf having taeniopteroid venation are arranged in close spiral bearing anomocytic stomata. Anatomically vascular bundles are arranged in row, each surrounded by sclerenchymatous bundle sheath showing diploxylic condition that is a central protoxylem, a larger centripetal primary metaxylem mass and a small arc of centrifugal mass. The stiff coriaceous leaves are borne in the form of bunch in the apical portion of slender shoots which usually emerge in the leaf axils of long shoots. The plants were deciduous dropping off leaves in their entirety.

Plate 2.1

Plate 2.1.

A. Reconstruction of *Pentoxylon* - plant showing its tree habit. x0.18.
B. Long shoot surface showing oval scars of type - 3. slender shoots subtended by leaf scars. x0.74.
C. T.S. of long shoot of *Pentoxylon sahnii*. x4.41.
D. T.S. of type - 3 short shoot of *Pentoxylon sahnii* SRIVASTAVA showing xylem plates. x5.88.
E. Type - 3 short shoot showing bulging leaf cushions. x2.9.
F. Leaf of *Nipaniophyllum hobsonii* BOSE et al. showing venation. x0.74.
G. T.S. of petiole of *Nipaniophyllum* sp. x18.38.
H. T.S. of lamina of *Nipaniophyllum* leaf. x18.38.
I. *Nipaniophyllum* leaf showing distribution of stomata. x22.06.
J. *Nipaniophyllum* leaf showing stomata and epidermal cells. x183.83.
K. T.S. of *Nipaniophyllum* leaf showing vascular bundle of midrib. x183.83.
L. Tangential longitudinal section of *Sahnia nipaniensis* VISHNU-MITTRE. x5.88.
M. Pollen of *Sahnia nipaniensis* VISHNU-MITTRE. x220.59.
N. Type - 2. short shoot bearing *Carnoconites compactus* SRIVASTAVA. x0.74.
O. *Carnoconites compactus* cone showing ovules. x1.47.

The male cone *Sahnia nipaniensis* VISHNU-MITTRE (1953) abscissed from base has been borne on a caducous short shoot. The shoot surface is covered by helically arranged leaf-cushions and the grooves between the cushions possess unicellular hairs. The microsporophylls more or less in a whorl are branched radially or unbranched spirally or irregularly arranged on conical-cylindrical receptacle, each balloon-shaped or globose sporangium stalked, present in two lateral rows. Sporangia enclose boat-shaped elliptical or circular monocolpate pollen with reticulate exine, typically of cycadean type.

Female cone *Carnoconites* (SRIVASTAVA 1944) borne on woody short shoot, spirally attached to the peduncle with a pedicel. Peduncle in the upper part shows a central cylinder of about ten collateral bundles and in the cortex around there are always five groups of bundles which are supposed to be of supply bundles to the pedicels of five cones. Each cortical group consists of three bundles in which middle one is smaller than two lateral ones. Ovules with micropyle point outwards. Seeds platyspermic, spirally attached, outer fleshly sarcotesta and inner stony layer well developed. Nucellus free from integument, apically nucellar membrane projects into the micropyle. Vascular strand enters from chalazal end and terminates below the base of nucellus. Few seeds are with embryo. Two species recovered from Rajmahal Hills are *C. compactus* (SRIVASTAVA 1944) and *C. rajmahalensis* WIELAND (BOSE et al. 1985) have been differentiated in the nature of compact and lax arrangement of their seeds directly attached to axis. Both species of seed cones were borne on peduncles with an exception that *C. compactus* bore long pedicels where as the elongated cones of *C. rajmahalensis* possessed short pedicels. The seed of *C. rajmahalensis* as compared to *C. compactus* are more in number and smaller in size having thin sarcotesta. Further the well developed fleshy layer of these seeds after fertilization have been interpreted as to be for attracting the insects whereas the sclerotesta of these seeds must have been for protection as well as for dissemination or dispersal.

Habitat

The ongoing account of various plant organs belonging to pentoxylopsids is suggestive of the occurrence of two species of *Pentoxylon*-plant that existed during that period in the terrain of Rajmahal Hills forest. The reason being that the leaf and seed cone gen-

era are represented by two distinct species associated with other plant groups like pteridophytes and conifers. Cycadophytes are less frequent in southern part of the basin. From the entire floristic scenario of *Nipania*, it appears that the *Pentoxylon* - plant occupied the understorey in association of cycadophytes where as the conifers etc. were slightly at higher altitude. Additionally, it is worthwhile to point over here that most of the chert blocks when were examined it was found that where there was overwhelming dominance of pentoxylopsids, rarely any coniferous remains could be marked on those chert slices. This observation support for pentoxylopsids growing in the community of moisture loving plants, is also in the fitness of contention (BOSE et al., 1985) that *Pentoxylon*-plant grew beside water.

However, it could be visualized that the advent of pentoxylopsids mark a definitive floral change towards the late part of Jurassic or Early Cretaceous when this new plant group with different phyto-communities existed, and that is a subject now to ponder over it. In northern part such as (Onthea, Sakrigalighat and Mandro) of Rajmahal Basin, pentoxylopsids remains have been recovered where cycadophytes frequently occur, though their preservation is quite different probably due to taphonomical factors. Conclusively, the flora flourished along the lake margin on volcanic terrain as a part of mixed deciduous sub-tropical forest in humid climate.

Phylogenetic Interpretations

Pentoxylon-plant belongs to an unique group of gymnosperm because:

1. Secondary wood of *Pentoxylon* stem having been of coniferous type but without xylem parenchyma.
2. Bearing single-type of tracheidal pitting and different raypit field.
3. Leaf exhibit anomocytic-type of stomata having vascular traces with diploxylic condition identical to *cycads* but in its direct leaf traces, the leaf differs from cycads having girdle leaf traces.
4. Microsporophylls are borne on cylindrical receptacle showing branching, at times unbranched sac-like microsporangia quite distinct from bennettitalean synangia.
5. The ovules are borne directly on the cone axis without having any bract, ovuliferous scales or interseminal scales of perianth, an unique nature among the gymnosperm group as regards the mode of attachment of ovules.

Distribution in space and time

Besides extensive occurrence of pentoxylopsids in Nipania beds of Rajmahal Hills, India, HARRIS (1962) described *Carnoconites (C. cranwelli)* from the *Taeniopteris* bed at Port Waikato, New Zealand which has been dated as Tithonian. Later, WHITE (1981) reported male and female cones from Jurassic of Talbragar Fish Bed, New South Wales, Australia. The main trunk of *Pentoxylon*-plant was recoreded by ROZEFELDS (1982) from south east Queensland of Australia. Lately, DRINNAN and CHAMBER (1985) published a comprehensive work of pentoxylopsids (*C. cranwelli, Sahnia laxiphora* and *Taeniopteris daintreei*) from Early Cretaceous of Koonwarra Whitelaw beds of Victoria, Australia.

The palaeogeographic distribution of pentoxylopsids is suggestive of that this plant-group flourished well in the eastern part of Gondwanaland during Jurassic-Cretaceous period. Recent finding of *Taeniopteris* sp. and *Carnoconites llambiasii* by CESARI et al. (1998) indicate the occurrence of *Pentoxylales* from Early Cretaceous bed of the Byers Peninsula, South Shetland Island, Antarctica.

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